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Arboreal lichens in successional forests on southern Vancouver Island

K.A. Enns, J. A. Trofymow, and D.M. Goodman

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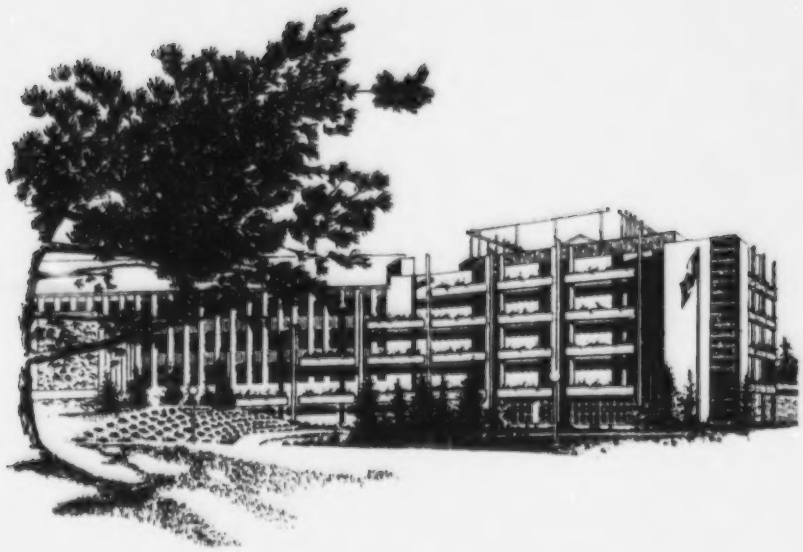

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Contents

Abstract iv

Résumé iv

Acknowledgements v

Introduction 1

Methods 1

- Description of sites 1
- Sampling and identification of lichens 1
- Data analysis 3

Results 3

- Comparison of lichen communities in stands of four age-classes 5
- Comparison of lichen communities in the CWHxm and CWHvm biogeoclimatic subzones 5
- Comparison of lichen communities on five tree species 5
- Comparison of lichen species richness on young branches and on older branches and boles at Koksilah 5

Discussion 10

- Effects of sampling design 10
- Comparison of lichen communities in the CWHxm and CWHvm biogeoclimatic subzones 11
- Comparison of lichen communities on young branches in stands of four age-classes 11
- Comparison of lichen abundance on several tree species 11
- Conservation of lichen diversity 12

Conclusions 12

References 13

Appendices 15

Abstract

Changes in the relative abundance and diversity of arboreal lichens on young branches were studied on chronosequence plots established on southern Vancouver Island by the Canadian Forest Service at four sites in the Very Dry Maritime (CWHxm) and four sites in the Very Wet Maritime (CWHvm) Coastal Western Hemlock (CWH) biogeoclimatic subzones. A total of 32 stands were sampled. Each site had a chronosequence of stands of four age classes: old growth (176-435 years), regeneration (3-9 years), immature (32-43 years), and mature (66-99 years) stands. The branches examined had been sampled for foliar nutrient analysis study being conducted on these sites. Entire branches were collected from the upper crown of three trees of each species found in each plot. To supplement this undirected sample, a more directed sample was conducted at one site in the CWHxm (Koksilah) where lichens on older windfall branches and on the bark were also sampled. Lichen individuals were counted and identified to the species level. Many young branches had no lichens or had recent immigrants only. On young branches or older substrates, more species were found in mature or old-growth plots than in immature or regenerating plots. Branches from old-growth plots had more highly structured and richer communities, and more species of crustose lichens. There were more species of lichens on Douglas-fir, which predominates on the drier sites, than on other conifers, and the drier sites in the CWHxm had a richer lichen flora than those in the wetter CXHvm.

Résumé

Une étude des variations de l'abondance et de la diversité relatives des lichens corticoles sur de jeunes branches a été effectuée dans des chronoséquences établies dans le sud de l'île de Vancouver par le Service canadien des forêts, plus précisément à quatre endroits dans la sous-zone Maritime très sèche (CWHxm) et à quatre endroits dans la sous-zone Maritime très humide (CWHvm) de la zone biogéoclimatique côtière de la pruche de l'Ouest (CWH). Des échantillonnages ont été menés dans 32 peuplements au total. Il y avait à chaque endroit une chronoséquence de quatre classes d'âge : peuplements vieux (176-435 ans), en régénération (3-9 ans), jeunes (32-43 ans) et mûrs (66-99 ans). Les branches examinées avaient fait l'objet d'échantillonnages dans le cadre d'une étude des éléments nutritifs des feuilles menée aux mêmes endroits. Des branches entières ont été prélevées dans la partie supérieure du houppier de trois arbres de chaque essence dans chaque parcelle. En complément de cet échantillonnage aléatoire, un échantillonnage plus ciblé a été réalisé à un endroit dans la sous-zone CWHxm (Koksilah), où l'on a également prélevé des échantillons de lichens sur de vieilles branches abattues par le vent et sur l'écorce. Les lichens ont été comptés et identifiés jusqu'au niveau de l'espèce. Beaucoup de jeunes branches étaient dépourvues de lichens ou ne portaient que des immigrants récents. Les jeunes branches ou les substrats plus âgés accueillaient davantage d'espèces dans les parcelles aux peuplements mûrs ou vieux que dans les parcelles aux peuplements jeunes ou en régénération. Les branches prélevées dans les peuplements vieux accueillaient des communautés plus riches et à structure plus complexe ainsi que davantage d'espèces de lichens crustacés. On a observé un plus grand nombre d'espèces de lichens sur les branches de sapin de Douglas, essence dominante aux stations sèches, que sur celles des autres conifères, et la flore lichénique était plus riche aux stations sèches de la sous-zone CWHxm qu'aux stations de la sous-zone CWHvm.

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Introduction

There have been few studies of arboreal lichens in the Pacific Northwest (Pike et al. 1977) and those on Vancouver Island have been restricted in scope. The taxonomic work of Noble (1982) was restricted to the dry Douglas-fir, *Pseudotsuga menzeisii* Mirb. Franco, forests of southern Vancouver Island. The deficiency of lichens in second-growth forests on Vancouver Island has been considered a problem mainly because it is a food source for black-tailed deer, *Odocoileus hemionus* subsp. *columbianus* (Nyberg and Janz 1990). Thus, most comparisons of lichens in old growth and second growth have been of species used as forage by deer or elk, primarily *Alectoria sarmentosa* in clearcuts and in small areas at the edge of mature forests. As concerns about conservation of lichen diversity or ecosystem function have been secondary, more knowledge of the biology of the lesser known canopy lichens is needed to sustain their diversity and functions in managed forests.

The epiphytic cryptogams — lichens, mosses, liverworts and hornworts — are probably among the biota most sensitive to clearcutting. Many of these small non-vascular plants require large, old coniferous trees as a substrate (Barkman 1958), and many need upper crown continuity for dispersal (Wolfenbarger 1975; Esseen 1985). Some species require bark substrates that are only found on trees of specific ages. Many require specific microclimates, such as frequent wet-dry cycles in cool but brightly lit crowns (Brodo and Hawksworth 1977). Clearcutting large areas of old growth could result in a decline in lichens with poor dispersal capability (Lesica et al. 1990). On eastern Vancouver Island, arboreal lichens are least abundant in stands 10 - 35 years old (Stevenson and Enns 1992). Although fragments of *A. sarmentosa* can disperse as far as 1200 m from the cutblock edge (Stevenson and Enns 1992), many small foliose and crustose lichens are dispersed much shorter distances as fragments are dispersed by birds or insects, or as spores (Esseen 1983).

To further understand what changes occur in lichen communities following clearcutting and how lichen communities recover in second growth, comparisons can be made between lichen communities in remnant old-growth stands with those in adjacent young and maturing second-growth stands. This report compares the abundance and numbers of species of lichens (richness) on young branches in an undirected sampling of chronosequences of stands at eight sites on Vancouver Island in 1995, and lichen richness in a directed sampling of older branches and boles at a single site (Koksilah) in 1996. The objective of this study was to determine if abundance and richness of lichen species was related to stand age.

Methods

Description of sites

Lichens on young branches were collected from 32 stands at eight sites in the Coastal Western Hemlock (CWH) biogeoclimatic zone on southern Vancouver Island. These "coastal forest chronosequences", described by Trofymow et al. (1997), were established to investigate the impacts of converting old-growth forests to managed forests and how various ecosystem attributes change during secondary stand succession. Four of the sites (Victoria Watershed South, Victoria Watershed North, Koksilah, Nanaimo River) were in the Very Dry Maritime subzone (CWHxm) and four (Renfrew, Red/Granite Creek, Nitinat, Klanawa) were in the Very Wet Maritime subzone (CWHvm) (Figure 1). Each site contained a chronosequence of four stands of different ages (reference year 1990): old growth (176 at Red/Granite Creek, and 234 to more than 450 years at the other sites), regeneration (3-9 years), immature (32-43 years), and mature (66-99 years). Stands were mid-slope and within a site stands were on similar slope and aspect and within 200 m of each other in elevation. The regeneration, immature and mature stands were all of clearcut and slashburn origin, except for mature stands at Koksilah and Klanawa which were of stand-destroying wildfire origin. Origin of the old-growth stands was unknown.

Sampling and identification of lichens

As part of the Coastal Forest Chronosequences project, in 1992 plots were established in each of the 32 stands and trees were marked and measured. Each plot consisted of four subplots each with a radius of 10 m, one in the center

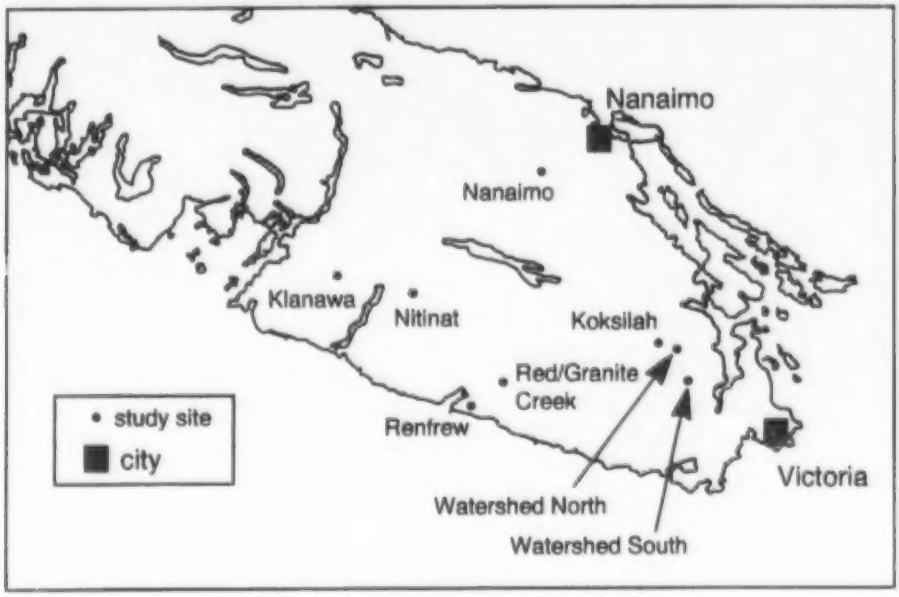

Figure 1. Location of Coastal Forest Chronosequence study sites on southern Vancouver Island.

and three others located 30 m from the center and 120° apart (Trofymow et al. 1997). In the autumn of 1995, overstorey foliage from trees in the 32 plots was sampled for foliar nutrient analysis. Trees were climbed or pole pruners were used to collect entire branches from the sixth to eighth whorl (counting from the top of the tree) from three trees of each species found in each of the 32 plots. Table 1 lists the tree species present in each plot. Branches were trimmed to retain only those portions of the branch less than 7 years old. A total of 218 trees were sampled. The effort expended to collect these branches was considerable considering the height of some of the trees in the old-growth plots; consequently, these branches were used as an undirected sampling of the arboreal lichen communities. Branches were placed in plastic bags and returned to the laboratory where they were kept at 2°C until processing. Branches were examined for lichens within one week of sampling.

To supplement the undirected sample, a second, directed sample of plots at the Koksilah site was completed in February 1996 in an attempt to maximize the number of lichen species collected. Branches that had fallen during a recent severe windstorm were collected within the plots in each of the four stands at the Koksilah site along with bark from boles. Twenty-five randomly chosen branches in each stand were assessed in the field for lichen richness, and ten of those 25 were chosen and returned to the laboratory for complete lichen species identification. In the regeneration stand, logging slash was collected instead of windfallen branches, but only arboreal lichens were surveyed; the occurrence of terrestrial lichens was not recorded. Branches in the old-growth plot ranged from 2 to 15 cm in diameter and 15 to 180 cm in length. The lower 200 cm of boles of 25 trees per plot were assessed for lichen species richness, and bark samples were taken from ten trees per plot for lichen species identification.

Mature lichens were identified to the species level using keys and descriptions from Noble (1982) and Goward et al. (1994). Juvenile lichens and fragments of immigrant lichens were also identified to the species level if possible. Identifications of some specimens were verified by Dr. F. Rhoades (University of Washington), Dr. B. Ryan (Arizona State University), and Ms. A. Ceska (University of Victoria). A consolidated list of all species identified in both the 1995 and 1996 sampling is provided in Appendix I.

Data analysis

Unless otherwise stated, analyses were performed with the aid of SAS (Statistical Analysis Software) software (SAS Institute 1985). To test for differences in lichen abundance (number of lichen individuals per branch) and richness (number of species) among age classes, analyses of variance were run using the generalized linear model as implemented in SAS PROC GLM (SAS Insititute 1985). The model included the main effects of biogeoclimatic subzone, age class, site, and the two-way interaction of subzone with age class. The assumption of homogeneity of variances was tested with scatter plots of residuals versus predicted values and of standard deviations versus means for the values of the dependent variable. Normality of residuals was tested using PROC UNIVARIATE (SAS Institute 1985). Main effects or interactions were removed from the model if they were not significant at a confidence level of 20%. Numbers of lichen individuals in different stand age classes and tree species were compared using Tukey's boxplots (Wilkinson et al. 1992).

Results

Most lichens were identifiable and are common in coastal forests, although many juveniles were only identifiable to the genus level. For example, *Parmelia sulcata* can be distinguished from *Parmelia squarrosa* by comparison of rhizine branches, but these were insufficiently developed to differentiate to the species level in some cases. Many lichens had not yet developed soredia, isidia, or fruiting structures. Many branches from young trees had no lichens (Table 1), or only fragments of recently dispersed *Bryoria pseudofuscescens* or *Alectoria sarmentosa*. *Alectoria vancouverensis*, a rare species (Goward et al. 1994), was found at Koksilah. The most species found on any single branch was 12. A complete list of lichen species found on the young branches sampled in each plot is provided in Appendix II.

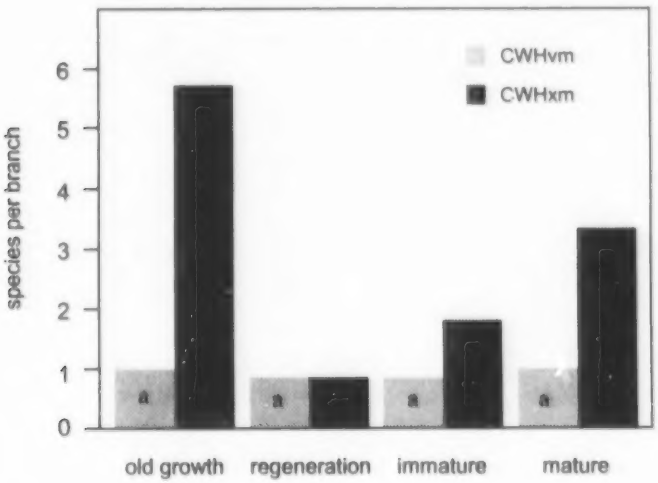

Figure 2. Mean number of lichen species per branch on young branches in old-growth (>200 years), regeneration (3-9 years), immature (32-43 years), and mature (66-99 years) stands at eight sites in the very dry maritime (CWHxm) and very wet maritime (CWHvm) Coastal Western Hemlock biogeoclimatic subzones (n=4 for each subzone, n=8 overall). Within subzones, bars labeled by the same letter are not significantly different in height according to a Duncan-Waller multiple comparison procedure, at a 95% confidence level. Data were weighted according to the relative abundance of each tree species, using stems per hectare for the regeneration plots, and basal area for the other age classes.

Table 1. Number of lichen individuals (In) and species (Sp) found on seven-year-old branches, and number of branches (Br) sampled, in stands of four age-classes at four sites in each of the very wet maritime (vm) and very dry maritime (xm) subzones of the Coastal Western Hemlock (CWH) biogeoclimatic zone.

Biogeoclimatic Subzone	Site	Tree Species[a]	Old Growth			Regeneration			Immature			Mature			Totals		
			Br	In	Sp	Br	In	Sp	Br	In	Sp	Br	In	Sp	Br	In	Sp
CWHvm	Klanawa	Ba	3	9	4	0	--	--	3	2	1	3	6	3	9	17	8
		Cw	3	1	1	0	--	--	3	0	0	0	--	--	6	1	1
		Hw	3	4	2	3	3	2	3	3	2	3	5	4	12	15	8
		All	9	14	5	3	3	2	9	5	3	6	11	6	27	33	12
	Nitinat	Ba	3	13	5	0	--	--	0	--	--	0	--	--	3	13	5
		Cw	3	2	1	0	--	--	3	1	1	0	--	--	6	3	1
		Dr	0	--	--	0	--	--	3	1	1	0	--	--	3	1	1
		Fd	0	--	--	0	--	--	3	4	2	0	--	--	3	4	2
		Hw	3	10	5	3	9	7	3	1	1	3	8	5	12	28	12
		All	9	25	7	3	9	7	12	7	4	3	8	5	27	49	13
	Renfrew	Ba	3	13	8	0	--	--	0	--	--	3	7	5	6	20	12
		Cw	3	1	1	0	--	--	3	0	0	3	1	1	9	2	2
		Dr	0	--	--	3	0	0	0	--	--	0	--	--	3	0	0
		Hw	3	12	8	3	1	1	3	1	1	3	8	5	12	22	9
		All	9	26	11	6	1	1	6	1	1	9	16	8	30	44	14
	Red/	Cw	3	2	2	0	--	--	3	0	0	0	--	--	6	2	2
	Granite	Dr	0	--	--	0	--	--	3	6	4	0	--	--	3	6	4
	Creek	Fd	0	--	--	3	1	1	1	3	3	0	--	--	4	4	3
		Hw	3	7	5	3	0	0	3	7	6	3	4	4	12	18	10
		All	6	9	6	6	1	1	10	16	10	3	4	4	25	30	10
CWHvm Total			33	74	18	18	14	8	37	29	13	21	39	14	109	156	21
CWHxm	GVWN[b]	Cw	3	6	3	0	--	--	0	--	--	3	4	3	6	10	6
		Fd	3	25	17	3	1	1	3	15	12	3	9	6	12	40	23
		Hw	3	9	7	3	0	0	0	--	--	0	--	--	6	20	7
		All	9	41	18	6	1	1	3	15	12	6	13	7	24	70	22
	GVWS[c]	Cw	3	3	1	0	--	--	0	--	--	3	5	6	6	8	6
		Dr	0	--	--	3	0	0	0	--	--	0	--	--	3	0	0
		Fd	3	18	15	3	0	0	3	1	1	3	11	5	12	30	16
		Hw	3	15	9	3	1	1	3	0	0	3	10	4	12	26	11
		Pw	0	--	--	3	0	0	0	--	--	0	--	--	3	0	0
		All	9	36	18	12	1	1	6	1	1	9	26	9	36	64	23
	Koksilah	Cw	0	--	--	0	--	--	3	3	1	0	--	--	3	3	1
		Fd	3	17	14	3	3	1	3	4	4	3	20	13	12	44	19
		Hw	3	16	8	3	0	0	0	--	--	0	--	--	6	16	8
		All	6	33	17	6	3	1	6	7	4	3	20	13	21	63	22
	Nanaimo	Cw	3	2	1	0	--	--	0	--	--	3	7	3	6	9	3
		Dr	0	--	--	0	--	--	1	0	0	0	--	--	1	0	0
		Fd	3	23	8	3	9	6	3	4	3	3	3	2	12	39	13
		Hw	3	18	12	3	7	7	0	--	--	3	18	14	9	43	22
		All	9	43	15	6	16	10	4	4	3	9	28	14	28	91	30
CWHxm Total			33	153	37	30	21	11	19	27	14	27	87	32	109	288	38
Grand Total			66	227	39	48	35	15	56	56	19	48	126	32	218	444	50

a Ba = amabalis fir; Cw = western redcedar; Hw = western hemlock; Dr = red alder; Fd = Douglas-fir; Pw = white pine

b GVWN = Greater Victoria Water District North

c GVWS = Greater Victoria Water District South

Comparison of lichen communities in stands of four age-classes

Branches in old-growth plots had more lichen individuals and species than branches in regeneration or immature plots (Table 1, Figure 2). Because richness and abundance were correlated, their relationships to age class and biogeoclimatic subzone were similar. Eighty-five percent of branches had only one individual per species present. Branches from regeneration and immature plots had a relatively scant lichen flora, consisting of species with rapid colonization rates and a tolerance for extreme conditions. These include the fruticose pendulous lichens such as *Usnea* and *Alectoria*, which disperse rapidly. Branches from mature and old-growth plots had more of the common, easily fragmented foliose lichens such as species of *Hypogymnia* and *Platismatia glauca*.

Comparison of lichen communities in the CWHxm and CWHvm biogeoclimatic subzones

There were twice as many lichen individuals in the CWHxm as in the CWHvm ($p=0.01$) (Table 1). This was also true within old-growth ($p=0.005$) and mature ($p=0.07$) plots, but not in immature ($p=0.46$) or regeneration ($p=0.72$) plots. Species richness was highest in mature and old-growth plots of the comparatively dry CWHxm (Fig. 2, Tables 2 and 3). Branches with juvenile colonies of *Hypogymnia enteromorpha* and *H. imshaugii* tended to support more mature specimens of *Platismatia glauca* and *Alectoria* spp. in the CWHxm, whereas in the CWHvm these species most often occurred as single juveniles, or not at all.

Comparison of lichen communities on five tree species

Compared to other tree species, Douglas-fir supported more lichen individuals in all age classes except regeneration (Figs. 3-6). On branches of old-growth trees, there were twice as many lichen individuals on branches of Douglas-fir (median=8) as on any other tree species (Figure 6). This difference was significant at $p=0.05$. A few branches of western hemlock (*Tsuga heterophylla*) also had many (8-12) lichen individuals. No branch of western redcedar (*Thuja plicata*) or amabalis fir (*Abies amabilis*) supported more than five lichen individuals. Specificity of lichens for tree species was dramatic only in old-growth plots. Tree species had similar numbers of lichen individuals per branch in younger plots, where, for example, immigrant fragments of *Alectoria* spp. were just as common on western hemlock as on Douglas-fir. Although western redcedar branches had the fewest lichen individuals, in mature plots this tree species did support relatively frequent small immigrant fragments of fruticose pendulous lichens. Amabalis fir branches from mature and old-growth plots tended to have shade-tolerant lichens and fewer lichen species than either Douglas-fir or western hemlock.

Comparison of lichen species richness on young branches and on older branches and boles at Koksilah

In each plot at Koksilah, any 5-10 of the 25 branches assessed supported the entire number of lichen species observed (Table 4). Older branches and boles had larger numbers of crustose species, whereas the younger branches had mainly fruticose and foliose species that dwell in the outer canopy. Several species found mid-stem and on outer branches dominated on older branches and boles. Species of *Cladonia* and *Peltigera* were found only on older branches and boles, as was *Hypocenomyce castaneocinerea*, a crustose lichen typically found on burned Douglas-fir bark. Species found on older branches or boles, but not on younger branches, such as *Peltigera degenii*, were mostly from lower boles of Douglas-fir. Only the larger or more mobile species such as *Platismatia glauca*, *Hypogymnia imshaugii* and *Bryoria friabilis* occurred on both young and older branches. These species are common in canopies of coastal Douglas-fir (Pike et al. 1977; Noble 1982). Lichens were more mature on older branches and on boles, so 26 species were positively identified on those substrates, compared to only 19 on younger branches, even though five times more young branches were sampled. Twelve mature species were collected on young branches, compared to 28 on older branches and boles.

In old-growth plots at the Koksilah site, older branches did not support many of the upper canopy juvenile lichens found on young branches. In the regeneration stand, a group of typical residual species including *Hypogymnia imshaugii*, *Hypogymnia enteromorpha*, and *Platismatia glauca* were found on Douglas-fir logging slash. In the

Table 2. Lichen species found on young branches in stands of four age-classes, in the very wet maritime Coastal Western Hemlock biogeoclimatic subzone (CWHvm). Number of individuals (In) and percentage of all species (%). Species names followed by "?" indicate some uncertainty in identification, in many cases because the specimen was juvenile.

	Old Growth (n=66)		Regen. (n=13)		Immature (n=25)		Mature (n=34)	
Species	In	%	In	%	In	%	In	%
Alectoria sarmentosa	15	23	5	38	3	12	7	21
Alectoria sp.			1	8	1	4		
black apothecia					3	12		
black fruiting body							1	3
Bryoria friabilis	2	3			3	12	1	3
Bryoria pseudofuscescens	5	8						
Bryoria sp.	1	2					2	9
crustose spp.	2	3	1	8			1	3
green crustose	2	3	1	8				
Homalothecium sp. ?							1	3
Hypogymnia enteromorpha					1	4		
Hypogymnia physodes	5	8					5	15
Hypogymnia sp.	4	6			4	16		
Isopterygium elegans	1	2						
Isothecium myosuroides	9	14	1	8			5	15
light green crustose					1	4		
Parmelia sp.					1	4		
Parmelia sulcata	2	3			2	8	1	3
Parmelia sulcata or *squarrosa*							1	3
Parmeliopsis ambigua ?	1	2						
Platismatia glauca	2	3			1	4	2	6
soredia	4	6			1	4		
Usnea sp.	3	5	2	15	1	4	3	9
Usnea fulvoreagens ?	1	2						
white crustose	6	9	1	8	3	12	3	9
white crust, black apothecia			1	8				
white crustose, possibly *Protococcus* sp.	1	2						
white green crustose							1	3

Table 3. Lichen species found on young branches in stands of four age-classes, in the very dry maritime Coastal Western Hemlock biogeoclimatic subzone (CWHxm). Number of individuals (In) and percentage of all species (%). Species names followed by "?" indicate some uncertainty in identification, in many cases because the specimen was juvenile.

	Old Growth (n=154)		Regen. (n=20)		Immature (n=26)		Mature (n=81)	
Species	In	%	In	%	In	%	In	%
Alectoria sarmentosa	29	19	7	35	5	19	17	21
Alectoria sp.	2	1						
Alectoria vancouverensis	5	3			1	1		
black apothecia							1	1
black crustose					1	1		
black disassociated crustose							2	2
bright green crustose	1	1						
Bryoria friabilis	4	3	1	5	1	1	5	6
Bryoria glabra	1	1						
Bryoria oregana			1	5			1	1
Bryoria pseudofuscescens	13	83	3	15	4	15	10	12
Bryoria sp.	5	3	2	10	1	4		
Cetraria chlorophylla	2	1						
Cetraria halei	4	3					3	4
clear surficial crustose	1	1						
cream crustose							1	1
crustose spp.	2	1					3	4
Esslingeriana idahoensis	1	1						
green crustose	3	2						
grey crustose	2	1						
grey non-rhyzinate foliose lichen							1	1
Hypogymnia duplicata	1	1						
Hypogymnia enteromorpha	8	5	1		3	12	3	4
Hypogymnia imshaugii	4	3			1	4	2	2
Hypogymnia physodes			1	5				
Hypogymnia sp.	5	3	2	10	3	12	9	11
Isothecium myosuroides							2	2
light green crustose	1	1						
Parmelia sp.			1	5			1	1
Parmelia sulcata	2	1			2	8		
Parmelia squarrosa ?	5	3					1	1
Platismatia stenophylla							1	1
Platismatia glauca	3	2	1	5	1	4	5	6
Platismatia herrei	13	8					1	1
Platismatia lacunosa	5	3					1	1
Platismatia sp.					1	4	2	2
soredia	2	1					1	1
Sphaerophorus fragilis	3	2						
Sphaerophorus globosus	1	1						
Sticta fuliginosa	1	1						
Tuckermannopsis orbata	1	1						
Tuckermannopsis platyphylla ?	4	3						
Tuckermannopsis sp.	1	1					1	1
Usnea plicata group							1	1
Usnea sp.	1	1			1	4	3	4
white crustose	16	10			1	4	3	4
white with black apothecia	2	1						

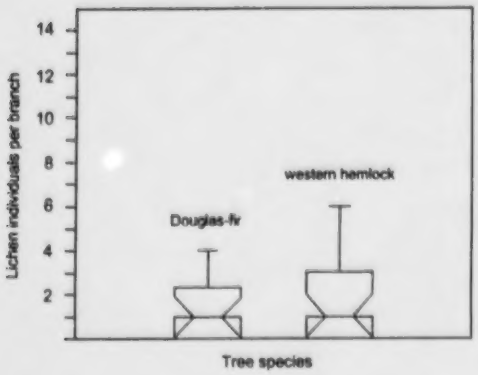

Figure 3. Abundance of lichen individuals on young branches (7 years old) of two tree species in regeneration stands (3-9 yr). The bee-waist in a boxplot indicates the median number of lichens per age class and the slopes of the bee-waist illustrate the 95% confidence limits on either side of the median value. When a bee-waist median is higher or lower than a neighboring boxplot, this indicates a significant difference between medians ($p < 0.05$). Extended bars or stars above (or below) the boxplots indicates the distribution of outlying numbers of lichens. A folded upper or lower portion of a boxplot indicates that the upper or lower range of data extends outside the confidence limits around the median.

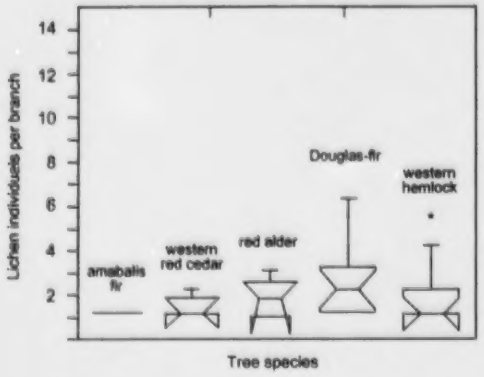

Figure 4. Abundance of lichen individuals on young branches (7 years old) of five tree species in immature stands (32-43 years old). See the legend of Figure 3 for an explanation of the boxplots.

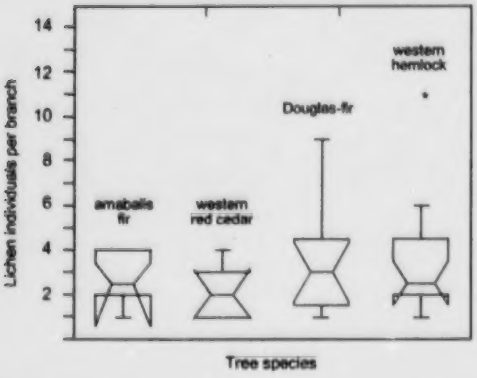

Figure 5. Abundance of lichen individuals on young branches (seven-year-old) of four tree species in mature stands (66-99 years old). See the legend of Figure 3 for an explanation of the boxplots.

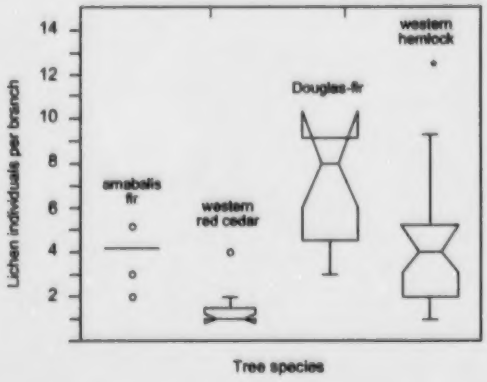

Figure 6. Abundance of lichen individuals on young branches (seven-year-old) of four tree species in old-growth stands (176-435 years old). See the legend of Figure 3 for an explanation of the boxplots.

Table 4. Lichen species found (X) on older branches and boles in stands of four age-classes, at the Koksilah site in the very dry maritime Coastal Western Hemlock biogeoclimatic subzone (CWHxm). Species names followed by "?" indicate some uncertainty in identification, in many cases because the specimen was juvenile.

Species	Old Growth	Regen.	Immature	Mature
Avonimia sp.?	X			
Alectoria sarmentosa	X	X	X	X
Alectoria vancouverensis	X		X	X
Baeomyces rufus? Sterile juvenile	X			
Bryoria capillaris	X			
Bryoria freemontii	X		X	
Bryoria friabilis	X			X
Bryoria fuscescens?	X		X	X
Bryoria glabra				X
Bryoria pikei	X			
Bryoria tortuosa ?				X
Bryoria trichodes subsp. *trichodes*	X			
Buellia punctata	X			
Buellia sp.				X
Cetraria chlorophylla	X			
Cetraria platyphylla	X			
Cladina rangiferina		X		
Cladonia bacillaris	X			X
Cladonia bacillaris juveniles				X
Cladonia carneola	X			
Cladonia coccifera	X			
Cladonia crispata				X
Cladonia sp. *sterile* juvenile	X	X		X
Cladonia squamosa	X		X	X
Diploschistes sp.				X
Hypenomyce scalaris?	X			
Hypocenomyce castaneocinerea	X			
Hypogymnia duplicata			X	
Hypogymnia enteromorpha	X		X	X
Hypogymnia imshaugii	X	X	X	X
Hypogymnia inactiva	X	X		X
Hypogymnia metaphysodes			X	X
Imshaugia aleurites	X			
Isothecium myosuroides				X
Lecidea cinnabarina				X
Melanelia elegantula	X			
Melanelia sp.?				X
multiple white apothecia			X	X
Ochrolechia laevigata				X
Ochrolechia oregonensis	X			
Ochrolechia sp.		X		X
Ochrolechia upsaliensis	X			
Omphalina sp.	X			
Parmelia sulcata			X	
Peltigera britannica				X
Peltigera canina		X		X
Peltigera dezenii			X	X
Platismatia glauca	X	X	X	X
Platismatia herrei	X		X	
Platismatia stenophylla	X		X	X
Stereocaulon tomentosum				X
Thelotrema lepadinum				X
unknown juvenile crustose				X
Xylographa sp?			X	

immature plot, 18 upper canopy and lower-stem, foliose and crustose species of lichens were found on older branches and boles, whereas 12 mature species were found on young branches. Most of these mature species also occurred on older branches or boles.

Discussion

Effects of sampling design

Amount of shade, tree species, canopy position, and distance to a source of propagules can all drastically affect relationships between stand age and lichen richness on branches (Lesica et al. 1990). Outer branches and stems have a subset of the total richness of the epiphytic lichen community, often representing the fastest growing, most rapidly colonizing species (Pike et al. 1977; Stone 1986). Richness of species observed in this study was low in comparison to that in similar forest sites on Vancouver Island (Brodo and Hawksworth 1977), probably because sampling was generally limited to young branches. Differences in canopy versus non-canopy lichen communities are more distinct in old growth and mature stands than in immature and regenerating stands, due to the time it takes for stratification and niche separation to occur in old-growth stands (Barkman 1958). This pattern was observed in the Koksilah chronosequence. If older branches and boles had been examined at all sites, it is likely that there would have been even greater differences in lichen species richness between stands less than 40 years old (regeneration and immature) and stands over 70 years old (mature and old growth). Since an unknown proportion of the total lichen richness was sampled (Figure 7), more extensive sampling would also be expected to reveal larger absolute differences in species richness between age classes and biogeoclimatic subzones.

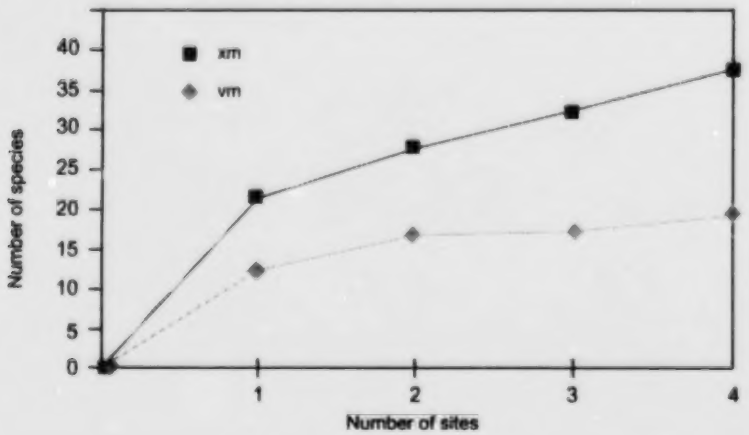

Figure 7. Number of species of lichens observed on young branches as a function of number of sites studied. Data are means of all possible combinations.

Sillett (1995) notes that there is often a trade-off between intensive and extensive sampling and concluded that intensive sampling was better for documenting species relationships, whereas extensive sampling is better for examining ecological influences on populations. More extensive sampling than that conducted in the Coastal Forest Chronosequence plots is recommended to help develop harvesting and forest management practices that would enhance the survival of those lichen species found almost exclusively in old-growth forests.

Comparison of lichen communities in the CWHxm and CWHvm biogeoclimatic subzones

The very wet maritime subzone (CWHvm) and the very dry subzone (CWHxm) of the Coastal Western Hemlock biogeoclimatic zone have distinct lichen communities. Noble (1982) attributes these differences in species composition mostly to climate, as do Brodo and Hawksworth (1977). The climate of the CWHvm is wetter and slightly cooler than the CWHxm (Green and Klinka 1994). The CWHvm has 2787 mm of annual precipitation and a mean annual temperature of 8.2°C, compared to the CWHxm which has 1750 mm of annual precipitation, a mean annual temperature of 9.1°C, and extended dry periods in summer months. The more extreme wet-dry cycles in the CWHxm may contribute to a greater richness of canopy dwelling lichens. Brodo and Hawksworth (1977) suggest that since lichens are xerophytic they form more diverse communities where they are exposed to sunlight and frequent wet-dry cycles. These authors also found quite different Bryoriad communities in the Coastal Douglas Fir (CDF) biogeoclimatic zone (*Bryoria fuscenscens*, *B. freemontii*, *B. friabilis* and *B. tortuosa*) and the Coastal Western Hemlock (CWH) zone (*Bryoria tricodes*, *B. bicolor*, *B. tenuis*, *B. capillaris* and *B. glabra*). The CWHxm plots had some species of each of these groups, while the CWHvm plots had only one of these species, *B. friabilis*. Branches with juvenile colonies of *Hypogymnia enteromorpha* and *H. imshaugii* tended to have more mature specimens of *Platismatia glauca* and *Alectoria* spp. associated with them in the CWHxm, whereas in the CWHvm, these species most often occurred as single juveniles or not at all. This observation indicates that, especially in lichen-rich dry sites, diversity is influenced by habitat suitability and succession (Stone 1986).

Comparison of lichen communities on young branches in stands of four age-classes

It is commonly assumed that clearcutting reduces the diversity of structures that are substrates for lichens and that this reduced structural diversity eventually leads to reduced richness of lichen species in mature forests (Noss and Cooperrider 1994, Goward 1994).

Lichens had dispersed into the regeneration stands, but lichen colonies there were insignificant in comparison to the species richness and abundance of lichens in older plots. The size of clearcuts, proximity to a source of propagules, and substrate characteristics are all likely reasons for the much lower diversity of lichens in regeneration plots. The four stands in each chronosequence were matched as closely as possible for stand history and for ecological features that are independent of stand age. However, the size of the openings from which the regeneration, immature and mature plots developed and the distance of the plots to old growth was not controlled and varied among sites. For example, the regeneration plot at Koksilah was more than 100 m from a source of lichen propagules, whereas plots in the immature and mature stands were within 50 m of old-growth stands or veteran trees. Large, common lichens like *Alectoria* and *Bryoria* spp. are easily dispersed and were consistently found in regeneration plots, but not in substantial numbers compared to mature stands.

The results of this study support those of Lesica et al. (1990), who found that: (i) some lichen species were restricted to old-growth and mature forests; (ii) there were fewer species of lichens in second growth than old-growth forests; (iii) *Cladonia* spp. were more abundant in mature and old-growth stands; (iv) few species were restricted to second growth or to immature stands; and (v) some species occurred in stands of all ages.

Comparison of lichen abundance on several tree species

Douglas-fir supported more lichen species and individuals than did the other tree species, probably because they were the dominant trees in the CWHxm where lichens were more abundant than in the CWHvm. Douglas-fir retains its bark which becomes thick and deeply furrowed with age while western redcedar, western hemlock and amabilis fir have stringy or scaly bark which is more easily shed (Farrar 1995). The bark of Douglas-fir thus provides a more stable substrate for lichens so as trees age they would tend to accumulate lichen species which dispersed poorly or grew slowly. The few branches of western hemlock that supported high numbers of lichen individuals indicates that more samples are needed to accurately describe the distribution of lichens on western hemlock, and suggests that western hemlock may support more lichens than western redcedar or amabalis fir. It has been observed elsewhere (Bird and Bird 1973) that lichens are scarce on western redcedar branches.

Conservation of lichen diversity

Will stands that regenerate following clearcutting eventually develop lichen communities similar to those of old growth? This study suggests that lichen communities will recover given sufficient time and proximity to older stands with complex lichen communities. Development of conservation strategies may require additional knowledge of how lichen communities recover in stands that regenerate after natural disturbances. Abundance of lichen individuals and diversity of lichen species in second-growth stands might be enhanced by inoculation, retention of lichen-rich trees during harvesting, and modifications in stand management to allow for development of more complex lichen communities. Second growth with some Douglas-fir will support a richer epiphytic community than pure stands of western hemlock, or stands of western hemlock and western redcedar.

Conclusions

On southern Vancouver Island, there were fewer lichen individuals and fewer species of lichens in regeneration and immature stands than in mature and old-growth stands.

Old-growth stands, especially Douglas-fir stands in the CWHxm, had more diverse and variable lichen communities than younger stands.

Young branches of Douglas-fir support more lichen individuals than young branches of other species of trees, although western hemlock had a tendency for occasional branches to bear larger numbers of individuals, especially in mature and old-growth stands.

Trees in the drier Coastal Western Hemlock biogeoclimatic subzone (CWHxm) had more lichen individuals on young branches than those in the wetter subzone (CWHvm).

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Appendices

Appendix I. Consolidated lichen species list from the 1995 sampling of young branches at all sites and the 1996 sampling of older branches and boles at Koksilah.

Species	Authority	Reference for identification (authority)
Agonimia sp.	Zahlbr.	Goward et al. 1994
Alectoria sarmentosa	(Ach.)	Noble 1982[a]
Alectoria vancouverensis	(Gyeln.) Gyeln. ex Brodo & D. Hawksw.	Noble 1982
Baeomyces rufus	(Huds.) Rebent	Thomson 1967
Bryoria capillaris	(Ach.) Brodo & D. Hawksw.	Noble 1982
Bryoria freemontii	(Tuck.) Brodo & D. Hawksw.	Noble 1982
Bryoria friabilis	Brodo & D. Hawksw.	Noble 1982
Bryoria fuscescens	(Gyeln.) Gyeln. ex Brodo & D. Hawksw.	Noble 1982
Bryoria glabra	(Mot.) Brodo & D. Hawksw.	Noble 1982
Bryoria oregana	(Tuck. ex Nyl.) Brodo & D. Hawskw.	Noble 1982
Bryoria pikei	Brodo & D. Hawksw.	Noble 1982
Bryoria pseudofuscescens	(Gyeln.) Brodo & D. Hawksw.	Brodo and Hawksworth 1977
Bryoria tortuosa	(Merr.) Brodo & D. Hawksw.	Noble 1982
Bryoria trichodes subsp. trichodes	(Michx.) Brodo & D. Hawksw.	Brodo and Hawksworth 1977
Buellia punctata	(Hoffm.) Mass	Noble 1982
Cetraria chlorophylla	(Willd.) Vain	Noble 1982
Cetraria halei	Culb. & C. Culb.	McCune and Geiser 1997
Cetraria platyphylla	Tuck.	Goward et al. 1994
Cladina rangiferina	(L.) Nyl.	Noble 1982
Cladonia bacillaris	(Ach.) Nyl.	Thomson 1967
Cladonia carneola	(Fr.) Fr.	Noble 1982
Cladonia coccifera	(L.) Willd.	Noble 1982
Cladonia crispata	(Ach.) Flot.	Thomson 1967
Cladonia squamosa	(Scop.) Hoffm.	Noble 1982
Diploschistes sp.	Norman	Noble 1982
Esslingeriana idahoensis	Hale & Lai	Goward et al. 1994
Homalothecium sp.		Vitt et al. 1988
Hypocenomyce scalaris	(Ach.) M. Choisy	Goward et al. 1994
Hypocenomyce castaneocinerea	(R:as:anen) Timdal	Goward et al. 1994
Hypogymnia duplicata	(Sm. ex Ach.) Rass	Goward et al. 1994
Hypogymnia enteromorpha	(Ach.) Nyl.	Goward et al. 1994
Hypogymnia imshaugii	Krog	Goward et al. 1994
Hypogymnia inactiva	Krog (Ohlsson)	Goward et al. 1994
Hypogymnia metaphysodes	(Asah.) Rass	Goward et al. 1994
Hypogymnia physodes	(L.) Nyl.	Goward et al. 1994
Imshaugia aleurites	(Ach.) S.F. Meyer	Goward et al. 1994
Isopterygium elegans	(Brid.) Lindb.	Vitt et al. 1988
Isothecium myosuroides	Brid.	Vitt et al. 1988
Lecidea cinnabarina	Somm.	Vitt et al. 1988
Melanelia elegantula	(Zahlbr.) Essl.	Goward et al. 1994
Ochrolechia laevigata	(R:as.) Vers.	Noble 1982
Ochrolechia oregonensis	H. Magn.	Noble 1982
Ochrolechia upsaliensis	(L.) Mass.	Noble 1982
Omphalina sp.	(Quel)	F. Rhoades (pers. comm.) (Hawksworth et al. 1995)[b]
Parmelia squarrosa	Hale	Goward et al. 1994
Parmelia sulcata	Taylor	Goward et al. 1994
Parmeliopsis ambigua	(Wulfen in Jacq.) Nyl.	Goward et al. 1994
Peltigera britannica	(Gyelnik) Holtan-Hartwig & T/onsb.	Goward et al. 1994
Peltigera canina	(L.) Willd.	Goward et al. 1994
Peltigera degenii	Gyelnik	Goward et al. 1994
Platismatia glauca	(L.) Culb. & C. Culb.	Goward et al. 1994
Platismatia herrei	(Imsh.) Culb. & C. Culb.	Goward et al. 1994
Platismatia lacunosa	(Ach.) Culb. & C. Culb.	Goward et al. 1994
Platismatia stenophylla	(Tuck.) Culb. & C. Culb.	Goward et al. 1994
Protococcus sp.		F. Rhoades (pers. comm.)
Sphaerophorus fragilis	(L.) Pers.	Vitt et al. 1988 (Index of Fungi 4:581)[b]
Sphaerophorus globosus	(Huds.) Vain	Noble 1982
Stereocaulon tomentosum	Fr.	Vitt et al. 1988
Sticta fuliginosa	(Hoffm.) Ach.	Goward et al. 1994
Thelotrema lepadinum	Ach.	Noble 1982
Tuckermannopsis orbata	(Nyl.) M.J. Lai	F. Rhoades (pers. comm.) (CAB Index of Fungi 5:1411)[b]
Tuckermannopsis platyphylla	(E. Tuckerman) M.E. Hale in Egan	F. Rhoades (pers. comm.) (CAB Index of Fungi 5:790)[b]
Usnea fulvoreagens	(R:as.) Mot. s. lat.	Noble 1982
Usnea plicata group	(L.) G.H. Weber ex F.H. Wiggers	F. Rhoades (pers. comm.) (CAB Index of Fungi 5:561)[b]
Xylographa sp.	(Fr.) Fr.	F. Rhoades (pers. comm.) (Hawksworth et al. 1995)[b]

[a] Most of Noble 1982 authorities are from Hawksworth et al. 1980; author abbreviations from Sayre et al. 1964; N. American endemics from Hale and Culberson 1970.

[b] Authority names for these species or genera are from the reference (in brackets) following the reference for identification.

Appendix II. Numbers of individuals of each lichen species found on young branches in each of the 32 plots sampled in 1995. See text for full site names. Plot numbers are from Trofymow et al. (1997). Seral stages are rg – regeneration, im – immature, ma – mature, og – old – growth. Species names followed by "?" indicate some uncertainty in identification, in many cases because the specimen was juvenile.

	Victoria Watershed South				Victoria Watershed North				Koksilah				Nanaimo River				Renfrew				Red/Granite Creek				Nitinat				Klanawa			
	1	2	5	6	11	12	13	15	21	22	23	24	31	35	33	34	51	52	53	54	61	62	63	64	71	72	73	74	81	82	83	84
Lichen	rg	im	ma	og	rg	im	ma	og	rg	im	ma	og	rg	im	ma	og	rg	im	ma	og	rg	Im	Ma	og	rg	im	ma	og	rg	im	ma	og
Alectoria sarmentosa			7	6	1	2	4	7	3	3	3	5	3		3	12			4	1		2	1	3	3	1	2	7	2	1		4
Alectoria sp.								1																					1			
Alectoria vancouverensis				2		1		2				1																				
black apothecia															1			1								2						
black crustose						1																										
black disassociated crustose											2																					
black fungal fruiting body						1	1																								1	
bright green crustose								1																								
Bryoria friabilis														1	5	4										1		2		2	1	
Bryoria glabra																1																
Bryoria oregana													1		1																	
Bryoria pseudofuscescens		1	1			1		1		2	3	4	3	1	6	8				1								2				2
Bryoria sp.	1							2		1			2			2			1							1	1					
Cetraria chlorophylla			1									1																				
Cetraria halei								2			3	2																				
Clear surficial crustose lichen								1																								
cream crustose											1																					
crustose spp.		2						1				2			1		1							1								
Esslingeriana idahoensis								1																								
green crustose								3												1					1			1				
grey crustose								1				1																				
grey non-rhyzinate folious lichen							1																									
Homalothecium ?																															1	
Hyogymnia physodes																				1												
Hypogymnia duplicata				1																												
Hypogymnia enteromorpha	1	1	2			2	1	4			1	1	1			1						1										
Hypogymnia imshaugii			1			1		1			2	2																				
Hypogymnia long																1																
Hypogymnia physodes													1						3	3			1				1	1				
Hypogymnia sp.		2	1			2	3	2		1	1		2		1	1				2		4						1				
Isoptergium elegans																																1
Isothecium myosuroides		1													1				1	1				1	1			6			4	2
light green crustose																1													1			
Ochrolec. juvenile?																				1												
Parmelia sp.		1										2	1									1										
Parmelia squarrosa?		1													1																	
Parmelia sulcata			1					2				1		2		2				2		2					1					
Parmelia sulcata or *squarrosa*			1																1													
Parmeliopsis sp.																				1												
Platismatia glauca		1	3			1		2			1	4	1		3	4			2	2		1										
Platismatia herrei			1					3				1			1																	
Platismatia lacunosa											1																					
Platismatia stenophylla			1				1	1								1																
Platismatia sp.						1	1								1	2																
soredia		1	3																	3		1		1								
Sphaerophorus fragilis			1																													
Sphaerophorus globosus								1																								
Sticta fuliginosa			1																													
Tuckermannopsis orbata			2									1																				
Tuckermannopsis platyphylla?			1																													
Tuckermannopsis sp.											1					1																
Usnea fulvoreagens?																				1												
Usnea plicatagroup								1							1																	
Usnea sp.		2	6			1		6			1	4							2	3	1	1	1		1							
White crust, black apothecia																									1							
White crustose						1	1								2	1				2		1	1	1	1	1	2	1		1		2
White crustose, poss. Protococcus																				1												
White green crustose																															1	
White with black apothecia													1			1																
Grand Total	1	1	20	36	1	15	13	46	3	7	20	32	16	4	28	43	1	1	15	25	1	14	4	7	8	5	7	22	3	5	8	11